

Physiology of nitrogen assimilation by mycorrhiza

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INTRODUCTION

Mycorrhizal symbiosis results in a growth stimulation of mycorrhizal plants, particularly, when the soils are poor in nutritious elements. This positive effect is due to a mineral nutrition improvement, particularly the phosphate nutrition. However the interaction between mycorrhizal infection and nitrogen nutrition received less attention. But the favourable effect of symbiosis in nitrogen metabolism of the host plant was shown in natural and experimental conditions.

Mycorrhizal fungi can be involved in different stages of nitrogen metabolism : soil organic nitrogen breakdown, uptake and translocation to the host of soluble organic nitrogen forms (amino-acids) or mineral forms (NH_4^+ , NO_3^-) and in the assimilation of these last nitrogen sources.

1.- ORGANIC FORMS OF NITROGEN : BREAKDOWN, UPTAKE AND TRANSLOCATION

The first stage in organic nitrogen mineralisation breakdown occurs due to the action of proteases with release of soluble aminoacids which are absorbed relatively easily by plants.

The excretion of protease was shown in ectomycorrhizal fungi grown in pure culture as for *Pisolithus tinctorius* (RAMSTEDT and SÖDERHÄLL, 1983), *Cenococcum graniforme* (BOTTON, pers. com.) and *Hebeloma cylindrosporum* (SCHEROMM pers. com.). Proteolytic activities have been clearly observed on *Vaccinium corymbosum* plants with ericoïd mycorrhizas (READ, 1984). This ability is due solely to the endophyte as plants obtained aseptically have no proteolytic activity (READ, 1984). Similary STRIBLEY and READ (1980) showed that mycorrhizal infection enabled *Vaccinium macrocarpon* seedlings to use amino acids as a nitrogen source, as easily as ammonium.

The uptake and translocation of amino acids were observed for *Pinus sylvestris* associated with *Suillus variegatus* (MELIN and NILSSON, 1952 ; 1953) and also for beech mycorrhizas (CARRODUS, 1966). Recently SANGWANIT and BLEDSOE (1984) have shown that Douglas fir roots could absorb amino acids and that mycorrhizas by *Hebeloma crustuliniforme* increased this uptake.

2.- MINERAL FORMS OF NITROGEN : UPTAKE, TRANSLOCATION AND ASSIMILATION

2.1. Uptake and translocation of mineral nitrogen

Mineral compounds, ammonium and nitrate, represent the major source of assimilable nitrogen for higher plants and constitute the main nitrogen fertilizers.

If the loss of ammonium by leaching is minimised in relation to that of nitrate, in most soils, the uptake of this ion by plants is often limited by its diffusion rate in the soil (between those of nitrate and phosphate). This rate decreases even more when drought occurs. This relative immobility of ammonium suggests that mycorrhizal infection enhances the uptake of this ion, due to the increase in the volume of soil explored. Mycorrhizal *Vaccinium* plants absorb more ammonium than the non mycorrhizal controls (STRIBLEY and READ, 1974, 1976). The *Glomus mossae* hyphae can uptake and translocate to the host plant ammonium from a $^{15}(\text{NH}_4)_2\text{SO}_4$ source that is inaccessible to the roots (AMES *et al.*, 1983). Recent research on Sorghum associated with *Glomus mossae* suggest that the fungus enables mycorrhizal plants to absorb nitrogen from a source which is less accessible to non mycorrhizal plant roots (AMES *et al.*, 1983). However, the nature of the nitrogen source has not been clearly established.

The uptake rates of ammonium in forest trees whether mycorrhizal or not, are usually higher than those measured for nitrate (FRANCE and REID, 1978; HARLEY and SMITH, 1983). The same applies for ectomycorrhizal fungi for which net uptake fluxes are very high (Tab. 1). The intensity of these fluxes could explain the stimulation of ammonium uptake observed for mycorrhizal roots (RYGIEWICZ *et al.*, 1984a).

The research of CARRODUS (1965, 1966, 1967) on excised beech mycorrhizas showed that ammonium uptake depends on the products of metabolism and that it is influenced by the carbohydrates supply of the tissues. Exogenous glucose and fructose, absorbed before or at the same time as NH_4^+ both increase the uptake of this ion. Inhibitors of respiratory metabolism (NaNO_3 and 2-4-DNP) decrease the uptake of NH_4^+ by 70% (CARRODUS, 1966). The presence of ammonium stimulates dark fixation of carbon dioxide by mycorrhizas and most of the radioactivity is incorporated in the glutamine, which is detected mainly in the fungal sheath of mycorrhizas. These observations demonstrate the close correlation between ammonium uptake and the availability of carbohydrate destined to supply α -keto acids which are precursors of amino acids.

But beech mycorrhizas do not seem to absorb nitrate very much (CARRODUS, 1966). Generally speaking, uptake stimulation for nitrate is less definite (Tab. 1). However FRANCE and REID (1979) showed that mycorrhizas significantly stimulated NO_3^- uptake by pine roots and that mycorrhizas formed by *Pisolithus tinctorius* were more efficient for the nitrate uptake than

those formed by other fungal species. According to FRANCE (1980) the uptake ability of the anion, measured on *P. tinctorius* mycorrhizas was 7 times greater than that anticipated from the uptake abilities of each of the symbiotic partners alone. This suggests a synergic effect due to the formation of mycorrhizas. In most of these experiments the uptake fluxes are determined by measuring the quantities of ions (NH_4^+ or NO_3^-) disappearing from the medium for short periods of time. NH_4^+ penetration is caused by the passive accumulation force due to the difference in electrochemical potential. It is normal that the uptake rates of this ion are higher than that of NO_3^- , which usually move against a positive gradient of this potential. These results do not demonstrate the exclusive use of one or the other of the two forms of mineral nitrogen in the nutrition of these plants.

Tableau 1. Ammonium and nitrate uptake rates by mycorrhizal or non mycorrhizal woody plants and ectomycorrhizal fungi. The uptake rates are expressed in $\mu\text{mol.h}^{-1}.\text{g}^{-1}$ D.W.

	Plant species	NH_4^+	NO_3^-	REFERENCES
HOST PLANT	<i>Pseudotsuga menziesii</i>	3.8 - 6 ⁽¹⁾	0.6 - 0.8 ⁽²⁾	(1)RYGIEWICZ <i>et al.</i> , 1984a
	<i>Picea sitchensis</i>	4.0 - 6.0 ⁽¹⁾	0.6 - 1.0 ⁽²⁾	(2)RYGIEWICZ <i>et al.</i> , 1984b
	<i>Tsuga heterophylla</i>	1.8 - 4.0 ⁽¹⁾	0.8 ⁽²⁾	
	<i>Pinus radiata</i>	7.0 ⁽³⁾		(3)FLEWELLING, 1979
	<i>Pinus nigra nigricans</i>	2.5 ⁽⁴⁾		(4)MARTIN, 1982
	<i>Pinus pinaster</i>	0.65 ⁽⁵⁾		(5)PLASSARD <i>et al.</i> , this volume
FUNGI	<i>Hebeloma crustuliniforme</i>	310 ⁽⁶⁾	39 ⁽⁷⁾	(6)LITTKE, 1982
	<i>Laccaria laccata</i>	190 - 360 ⁽⁷⁾		(7)LITTKE <i>et al.</i> , 1983
	<i>Pisolithus tinctorius</i>	210 - 600 ⁽⁷⁾		
	<i>Hebeloma cylindrosporum</i>	150 ⁽⁵⁾	10 - 20 ⁽⁵⁾	
	<i>Cenococcum graniforme</i>	19 ⁽⁸⁾	43 ⁽⁸⁾	(8)GENETET, 1983
MYCORRHIZAS	<i>Fagus sylvatica</i> *	14 - 32 ⁽⁹⁾	0 - 1.0 ⁽⁹⁾	(9)CARRODUS, 1966
	<i>H. crustuliniforme</i> and			
	<i>Pseudotsuga menziesii</i>	7 - 9 ⁽¹⁾	0.6 - 1.4 ⁽²⁾	
	<i>Picea sitchensis</i>	6.5 - 9 ⁽¹⁾	0.6 - 1.4 ⁽²⁾	
	<i>Tsuga heterophylla</i>	3.8 - 7.8 ⁽¹⁾		

* fungal species associated with *Fagus sylvatica* were not determined

2.2. Assimilation of mineral nitrogen

22.1. Nitrate assimilation

Nitrate uptake by plants usually implies that these organisms possess assimilation enzymes of this ion, that is, nitrate and nitrite reductases.

For the endomycorrhizas V.A., HO and TRAPPE (1975) showed that the spores of different strains of *Glomus mossae* could reduce nitrate into nitrite. However research carried out on endomycorrhizal plants associated with this fungal species, show that the increase in nitrate reductase activity in the mycorrhizal tissues is an indirect result of infection *via* the increase in phosphate nutrition rather than a direct contribution of the fungus (OLIVER et al., 1983).

Table 2.- *In vivo* Nitrate reductase activities of roots and shoots of woody species. The activities are expressed in $\mu\text{mol.h}^{-1}.\text{g}^{-1}$ D.W.

Plant species	roots	shoots	references
<i>Pseudotsuga menziesii</i>	13,3 (1)		(1) HO and TRAPPE, 1980
<i>Pseudotsuga menziesii</i>	0,7 (2)	0,43 (2)	(2) BIG and DANIEL, 1978
<i>Pinus contorta</i>	3,28 (2)	1,57	
<i>Pinus pinaster</i>	1,0 (3)	0,1 - 0,2 (3)	(3) PLASSARD et al., this volume
<i>Pinus radiata</i>	1,93 (4)	Not detectable (4)	(4) ADAMS and ATTIWIL (1982)
<i>Eucalyptus regnans</i>	2,71 (4)	0,87 (4)	

Forest species, likely to be ectomycorrhizal, use nitrate to different degrees depending on the species and environmental conditions (VAN DEN DRIESCHE, 1978 ; FRANCE and REID, 1983). Nitrate reductase activity was detected for Angiosperms and Gymnosperms (Tab. 2). The activity measured in the roots is always greater than that in the shoots (Tab. 2) and usually the translocation of nitrogen in the xylem of woody plants seems to occur in an organic form (BOLLARD, 1958, 1960 ; PATE, 1973) : the root seems therefore to be the essential organ of assimilation of mineral nitrogen, before it is transported and redistributed in shoots.

Ectomycorrhizal fungi are usually grown *in vitro* on media containing only reduced nitrogen (LUPPI and FONTANA, 1967) and many species are capable of using ammonium (NORKRANS, 1950 ; LUNDEBERG, 1970 ; LITKE et al., 1983 ; FRANCE and REID, 1984). Most of the higher mycorrhizal basidiomycetes were considered unable to use nitrate (COCHRANE, 1958). However, the results obtained gave cause to suspect considerable inter and intraspecific variations (HARLEY and SMITH, 1983). Recent research (FRANCE, 1980 ; SALSAC et al., 1982 ; MENTION et PLASSARD, 1983) has in fact shown that a certain number of ectomycorrhizal species could develop satisfactorily exclusively in presence of nitrate ; they had similar growth on ammonium and nitrate

(MENTION and PLASSARD, 1983)

Table 3. Properties of nitrate and nitrite reductases from *H. cylindrosporum* and higher plants.

	Plant	Enzyme nomenclature	Reductant (DH ₂)	cofacteur	V _M (μmol.h ⁻¹ .g ⁻¹ MF)	Km (μM)			Ref
						NO ₃ ⁻ /NO ₂ ⁻	DH ₂	FAD	
Nitrate reductase	<i>H. cylindrosporum</i>	EC. 1.6.6.3.	NADPH	FAD	5 - 10	200	25	0,18	(1)
	Higher plants	EC. 1.6.6.1.	NADH	-	10 - 20	100-500	10	-	(2)
									(3)
Nitrite reductase	<i>H. cylindrosporum</i>	EC. 1.6.6.4.	NADPH MV	FAD	4 ^(a) 10 - 30 ^(b)	15-350	ND	ND	(4)
	Higher plants	EC.1.7.7.1	Ferredoxine	-	100 - 600	10	ND	-	(2)

(1) PLASSARD *et al.*, 1984a - (2) GUERRERO *et al.*, 1981 - (3) HEWITT *et al.*, 1979(4) PLASSARD *et al.*, 1984b -

(a) NADPH as reductant

(b) Methylviologen (MV) as reductant

ND = not determined,

The fungi studied which can grow in presence of nitrate must possess the enzymes necessary for the assimilation of this anion. HO and TRAPPE (1980) measured *in vivo* the nitrate reductase activities of 7 ectomycorrhizal species : they vary between 0.47 and 2.22 μmol.h⁻¹g⁻¹DW. The conditions of extraction and measurement of nitrate and nitrite reductases were investigated for *Hebeloma cylindrosporum* thalli (PLASSARD *et al.*, 1984 a and b). For nitrate reductase the NADPH is the electrons donor specific to the enzyme (like that of *Neurospora crassa* and *Aspergillus nidulans* - GARRETT and AMY, 1978), and the optimum measurement of the activity requires the presence of FAD. In these conditions the kinetic constants (V_M and Km) have the same order of magnitude as those measured for most of the higher plants (HEWITT *et al.*, 1979 ; GUERRERO *et al.*, 1981) (Tab. 3). However the nitrite reductase presents characteristics that are very different from the enzyme of higher plants. This enzyme is very labile *in vitro*, and its activity measured in presence of methyl viologen has the same order of magnitude as the fungal nitrate reductase activity. For the higher plants, this enzyme is stable *in vitro* and it is usually 10 to 20

times more active than the nitrate reductase. However, relatively low nitrite reductase activity of the fungus does not appear to limit NO_3^- assimilation because there is no nitrite in the thalli or in the culture medium. The fungus grown in the sole presence of NH_4^+ has the same activity (VIGNON, 1984), which suggests that the enzyme is not inducible by nitrate contrarily to what is observed for a filamentous ascomycete, such as *Neurospora crassa* or on the higher plants. There is no significant accumulation of nitrate in fungal cells, where the levels are always close to the millimole (MENTION et PLASSARD, 1983), and the values of nitrate uptake fluxes and those of nitrate reductase activity are always very similar (Fig. 1).

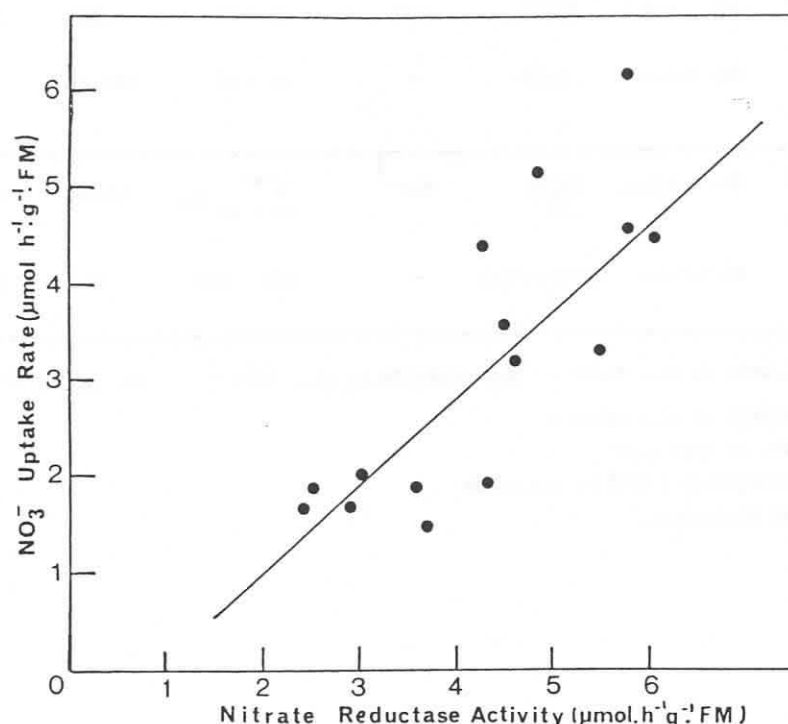


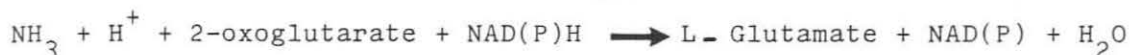
Figure 1. Relationship between nitrate reductase activity and NO_3^- uptake rates from *H. cylindrosporum thalli* ($y=0.93x - 0.985$; $r=0.72$)

So far, the measurement of the possible contribution of fungal enzymes in nitrate reduction by ectomycorrhizas has not yet been studied. However, the behaviour of a species such as *Pinus nigra nigricans* in presence of limestone and with nitric supply, illustrates the possible role of the fungus. In the absence of mycorrhizas, the tree cannot develop normally. The presence of the fungus reestablishes growth, probably by allowing nitrate assimilation and by an improvement in protein synthesis (CLEMENT *et al.*, 1977). This observation suggests a direct important role of fungal symbiont.

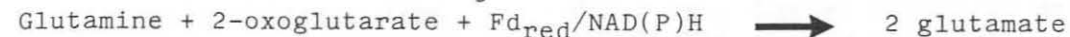
22.2. Ammonium assimilation

The incorporation of ammonium into organic compounds occurs via two pathways :

- (1) An NADP dependent-glutamate dehydrogenase which catalyses the animation of oxoglutarate into glutamate :



(2) The GS/GOGAT pathway with the sequential action of two enzymes : glutamine synthetase (GS) and glutamate synthetase (GOGAT) which catalyse the reactions:



This pathway predominates in higher plants (MIFLIN and LEA, 1980) but it appears that in higher fungi the GDH pathway predominates.

The assimilation of NH_4^+ has mainly been studied on an ectomycorrhizal fungus *Cenococcum graniforme* grown in pure culture. The primary NH_4^+ assimilation is catalysed by the sequential activity of GDH+GS. The GDH has been purified and found to have a negative co-operativity with respect to ammonium (K_{m1} : 2mM ; K_{m2} : 8 mM) (MARTIN *et al.*, 1983). Glutamine enters the ornithine cycle and leads to the synthesis of citrulline, and then arginine. Glutamine is therefore a transitory storage compound and soluble reduced nitrogen appears to accumulate mainly in the form of arginine (GENETET *et al.*, 1984 ; MARTIN *et al.*, 1985a). The use of methionine sulfoximine, which inhibits GS, suggests moreover that the formation of glutamine is a necessary stage for the later synthesis of proteins (GENETET *et al.*, 1984).

The assimilation of ammonium requires the supply of organic acids to act as precursors of amino acids. These precursors are supplied by the metabolism of glucose and the dark fixation of CO_2 , as is suggested by the observation of FRANCE (1980) and CARRODUS (1967).

In *C. graniforme*, the major carbohydrates produced from $[1\text{-}^{13}\text{C}]$ and $[6\text{-}^{13}\text{C}]$ glucose were mannitol and trehalose (MARTIN *et al.*, 1985b). The proportion of ^{13}C label entering the amino acid pools represented between 15 to 25% of the total soluble ^{13}C . Glutamate, alanine and arginine were next (MARTIN *et al.*, 1985b). It was concluded from the intramolecular ^{13}C enrichment of amino acids that the Krebs cycle and dark CO_2 fixation (phosphoenolpyruvate carboxykinase, pyruvate carboxylase and carbamoyl phosphate synthetase) supply high free amino acid pools.

In the ericoid fungus, *Pezizella ericae*, both GDH and GS are active. GDH appears to be operative when there are high concentrations, of NH_4^+ in the culture medium whereas GS has the major role at lower concentrations (St JOHN *et al.*, 1984).

GS and GDH activities were investigated on *Glomus mosseae* endomycorrhizal plants : GDH activity was low in all the tissues studied. However, non-infected roots of onion plants had low GS activities in relation to those measured in the shoots. When the roots were mycorrhizal, their GS activity increased significantly and this increase was probably due to the fungal enzyme (SMITH *et al.*, 1985).

The assimilation of ammonium in beech ectomycorrhizas seems to occur mainly by the GS/GOGAT pathway, and GDH in this case would only play a minor role (MARTIN *et al.*, 1985c). Two interpretations may be proposed in order to explain this results :

- the action of fungal GS and host GOGAT with translocation of glutamine and glutamate between the cells of the two partners, or
- the absorption of ammonium by the fungal hyphae and its translocation to the host cells where it is incorporated into the amino-acids by the usual GS/GOGAT pathway.

CONCLUSION

The first research showing the importance of mycorrhizal symbiosis in the nitrogen nutrition of host plants were carried out on ericoïd endomycorrhizas. (STRIBLEY and READ, 1974 ; 1976 ; 1980). Examples clearly demonstrating the importance of symbiosis for endomycorrhizas V.A. and ectomycorrhizas are less frequent. However, the indispensable association between a mycorrhizal fungus and *Pinus nigra nigricans* which ensures the adaptation of the tree to calcareous soils is a remarkable example (CLEMENT *et al.*, 1977).

Research in recent years has especially contributed to knowledge of pathways of mineral nitrogen assimilation by fungi. As far as ectomycorrhizas are concerned, only a few studies have been devoted to the nitrogen nutrition of forest trees. Results in this field are still fairly fragmentary and need to be completed. Observations made on fungal symbionts have shown that many species are able of effectively using nitrate, and have made it possible to establish the main characteristics of the corresponding enzymes. As opposed to what has been observed for Angiosperms, for which the physiology of nitrate assimilation has been studied most thoroughly, the fungi do not accumulate nitrate ; and for the basidiomycete at least, the nitrate reductase activity does not seem to be inducible by its NO_3 substrate. These observations raise several questions :

- What are the regulation mechanisms in NO_3^- assimilation ?
- Is nitrate uptake the limiting factor in the assimilation ?
- What are the mineral or organic soluble compounds which accumulate in the vacuole?

The pathway of ammonium assimilation and their relationships with carbonated metabolism have already been the subject of specific research for the ectomycorrhizal Ascomycete *C. graniforme*. These assimilation pathways seems to be quite as complex as those described for the higher plants. As opposed to what is at present accepted for the latter, GDH seems to ensure the initial incorporation of ammonium. The value of these data for a good understanding of the physiology of fungi is obvious, but they must be completed by the study of other species so as to draw general conclusions.

If studies on the physiology and biochemistry of the nitrogen nutrition of fungi are far from complete, those on the relationships between the two partners are few, and do not yet give us a clear idea of the mechanisms involved. To our knowledge, only one general scheme of relationship between carbon and nitrogen metabolism of the two partners has so far been proposed (FRANCE and REID, 1983). In order to better understand the biology of this symbiosis, it seems essential to extend research on the physiology of the two partners and on that of their association.

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